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EXPERIMENTS WITH THE ASTER-YELLOWS VIRUS FROM SEVERAL STATES[1]

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INTRODUCTION

IN 1929 THE AUTHOR[10] reported that *Cicadula divisa* Uhl. [*C. sexnotata* (Fall.)] transmitted yellows from naturally and experimentally infected varieties of celery to asters and from asters to celery in California. Kunkel[5] failed to infect 9 varieties of celery with the aster-yellows virus from New York by means of *Cicadula divisa*. In later papers the author[11,13] reported the transmission of yellows from naturally and experimentally infected varieties of carrot, parsley, and parsnip in California, but Kunkel[5] questions whether this disease is identical with aster yellows in New York, since the California aster-yellows virus is readily transmitted to celery and to *Zinnia elegans*, plants that are highly resistant if not immune to New York aster yellows.

Dorst,[1] who has made a study of the genus *Cicadula*, found that *Cicadula sexnotata* (Fall.) is a European species and that the American species is *Cicadula divisa* Uhl. Specimens of *Cicadula* were sent to Dorst by Kunkel from New York and by the writer from California, and all were determined as *Cicadula divisa*.

A review of the literature indicates that the celery yellows found in California probably occurs in other states. According to Linford,[7] aster and celery yellows first made its appearance in Utah during 1927.

Folsom[2] states that apparently the same disease as described by the author[10] was seen in southwestern Maine on an experimental farm,

[1] Received for publication February 7, 1934.

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where by systematic sweepings, the vector *Cicadula divisa* was caught for the first time in three years in which the work was carried on.

According to Vaughan and Foster,[19] aster yellows was found on celery in Wisconsin, but there was more infection in carrots than in celery or lettuce, when all three were growing adjacent to an experimental aster-yellows plot. Foster[3] planted about an acre of celery with asters between the rows at Madison, Wisconsin. He reports, "There were 3 celery plants in the entire field that developed symptoms that could be called typical aster yellows, without the twisting of the petioles. . . . In the same field I had a dozen large cages over celery plants in which colonies of *Cicadula divisa* were transferred early. This colony was collected from cages containing yellowed aster plants. Aster plants with yellows were also transplanted to the cages containing celery. These plants remained under the cages until late fall, and the hopper was present in large numbers at all times. None of the celery plants showed any of the yellows symptoms at any time."

Kunkel[6] experienced no difficulty in transmitting yellows to healthy aster and celery by means of *Cicadula divisa* from asters, celery, and carrots infected with California aster yellows, but failed to transmit the disease to zinnia. Yellows was also transferred from celery experimentally infected with California aster yellows, to healthy asters. California yellows on asters could not be distinguished by symptoms from the yellows disease prevalent on aster in New York. Kunkel came to the conclusion that celery yellows of California is not identical with aster yellows of New York.

Transmission experiments were performed, using *Cicadula divisa* occurring in California, with the aster-yellows virus obtained from New York, Indiana, and Wisconsin, carrot-yellows virus from Maine and Idaho, and celery-yellows virus from Utah, to determine whether healthy asters and celery could be experimentally infected with the disease. Tests were made to determine whether there are host-range differences between yellows viruses obtained from various states. Attempts were made to recover the virus from the experimentally infected plants. Experiments were also conducted to determine whether *Thamnotettix montanus* Van D., a newly discovered vector of California yellows, could transmit yellows from asters infected with the disease in New York and Wisconsin to healthy asters and celery. Attempts were also made to transmit yellows by feeding previously noninfective *Cicadula* on feeding solutions containing crushed infective leafhoppers which had fed on yellows-infected plants from New York and Wisconsin.

[3] Foster, A. C., letter to author dated February 18, 1931.

ASTER-YELLOWS VIRUS FROM NEW YORK

Through the courtesy of L. O. Kunkel, Rockefeller Institute for Medical Research, Princeton, New Jersey, three shipments of asters and salsify infected with yellows were received in good condition from New York.

TABLE 1

TRANSMISSION OF NEW YORK ASTER YELLOWS TO HEALTHY ASTERS AND CELERY BY *Cicadula divisa**

Experiment 1			Experiment 2		Experiment 3	
Insects transferred from New York aster yellows to healthy celery	Same insects transferred from celery to healthy asters	Same insects transferred from infected asters to healthy celery	Insects transferred from experimentally infected asters to healthy asters	Insects transferred from experimentally infected asters to healthy celery	Insects transferred from experimentally infected asters to healthy asters	Insects transferred from experimentally infected asters to healthy celery
Infections resulting						
−	+	−	−	3−	−	5−
−	+	−	+	1+ 4−	−	5−
−	+	−	−	5−	−	5−
−	+	−	+	1+ 4−	−	5−
−	−	....	....	....	....	....
−	+	−	+	1+ 4−	−	5−
−	+	−	+	5−	−	5−
−	+	−	+	1−	+	1+ 4−
−	+	−	+	1−	−	5−
−	+	+	−	1−	+	5−
−	−	....	....	....	....	....
−	+	....	....	....	−	5−
−	+	....	....	....	+	5−
−	−	....	....	....	....	....
−	+	....	....	....	+	1+ 4−
−	−	....	....	....	....	....
−	+	....	....	....	−	5−
—	—	—	—	—	—	—
	13+	1+	6+	3+	4+	2+
17−	4−	8−	3−	28−	9−	63−

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted.

Several experiments were conducted to determine whether asters, celery, carrots, and parsley could be experimentally infected with the aster-yellows virus from New York. In the first experiment previously non-infective male *Cicadula divisa* were fed on yellows-infected asters from New York for a period of 2 or 3 days and then 20 insects were transferred to each of 17 healthy celery plants. After feeding on the celery plants for a period varying from 19 to 27 days, each lot of leafhoppers was

transferred to a healthy aster plant. Ten of the 17 lots of leafhoppers, some of which had died, were again transferred from the inoculated asters to a second set of healthy celery plants for a period of 25 days. Table 1, experiment 1, shows that the first lot of celery plants remained healthy, 13 of the 17 asters inoculated became diseased, and 1 of the 9 celery plants in the second lot developed typical symptoms of yellows as described in a previous paper.[10] Celery plants used as a check or control remained healthy.

In the second experiment noninfective nymphs were exposed to 9 asters which had been experimentally infected with yellows in experiment 1. After the nymphs acquired the winged stage, lots of 5 to 35 males were transferred from each diseased aster to healthy asters and celery plants. Table 1 shows that in experiment 2, 6 of the 9 asters, and 3 of the 31 celery plants inoculated, showed typical symptoms of celery yellows.

In the third experiment 13 lots of leafhoppers after being exposed for a period of 8–28 days to 13 diseased asters from experiment 1, were transferred in groups of 5, to 13 healthy asters and 65 celery plants. Table 1, experiment 3, shows that 4 of the 13 asters and 2 of the 65 celery plants inoculated developed symptoms of yellows.

In the three experiments a total of 122 celery plants were inoculated with the New York aster-yellows virus, and 6 showed symptoms of celery yellows. The central leaves were chlorotic with a slight twisting of the petioles. Previously noninfective leafhoppers were exposed to the 6 celery-yellows plants and were then transferred to healthy asters and celery. The virus was repeatedly recovered by 3 lots of previously noninfective leafhoppers from only one celery-yellows plant, and typical symptoms of yellows developed with 3 asters. Previously noninfective leafhoppers, after feeding on the 3 diseased asters, failed to transmit yellows to 12 healthy celery plants.

It was decided to use larger numbers of leafhoppers with the salisfy infected with the aster-yellows virus from New York. Lots of 50 to 100 previously noninfective leafhoppers, after feeding on salsify infected with yellows for a period of 4 to 6 days, were transferred to successive healthy celery plants for periods of 2 weeks until all of the insects were dead. Eighty-five healthy celery plants were inoculated and 2 plants developed typical symptoms of yellows in the cages. Previously noninfective leafhoppers after feeding on the infected celery plants failed to transmit yellows to healthy asters and celery.

Carrots (*Daucus carota sativa*) showing symptoms of yellows have been reported by Whetzel,[20] Newhall,[8] and Kunkel[5] in New York, by Folsom[2] in Maine, by Zundel[21] in Pennsylvania, by Vaughan and Foster[19] in Wisconsin, and by the author[11,13] in California.

An experiment was conducted to determine whether varieties of carrots could be experimentally infected with the yellows virus from asters infected in New York by means of *Cicadula divisa*. Previously noninfec-

TABLE 2

INCUBATION PERIOD OF NEW YORK ASTER YELLOWS IN EXPERIMENTALLY INFECTED CARROTS AND RECOVERY OF VIRUS BY *Cicadula divisa*

Variety of carrot	Number of plants inoculated	Number of leafhoppers on each plant	Number of plants infected	Number of plants healthy	Incubation period in plant, days	Yellows transferred	
						From carrot to aster	From carrot to celery
Short White	1	20♂	1	0	15	−	−
	1	20♀	1	0	40	+	−
White Mastodon	1	20♂	1	0	40	−	−
	1	20♀	1	0	37	+	−
White Belgian	1	20♂	1	0	28	+	−
	1	30♀	1	0	18	+	−
Yellow Belgian	1	20♂	1	0	39	−	−
	1	30♀	1	0	53	−	−
Chantenay	1	20♂	1	0	24	−	−
	1	30♀	0	1	....	−	−
Danvers Half Long	1	20♂	1	0	39	+	−
	1	20♀	1	0	22	−	−
Early Scarlet Horn	1	20♂	1	0	21	−	−
	1	20♀	1	0	21	−	−
French Forcing	1	20♂	1	0	24	−	−
	1	30♀	1	0	42	−	−
Long Orange	1	10♀	1	0	16	−	−
	1	10♀	0	1	....	−	−
Nantes	1	20♂	1	0	39	+	−
	1	30♀	1	0	37	−	−
Oxheart or Guerande	1	20♂	1	0	28	−	−
	1	20♀	1	0	35	−	−
Total	22	.....	20	2	.....	6	0
Average	....	.....	....	....	30.9	....	....

tive leafhoppers, varying in number from 10 to 30 males or females, were exposed to aster-yellowed plants and then transferred to 3 white, 1 yellow, and 7 orange varieties of carrots, as indicated in table 2.

It is evident from table 2 that 20 of the 22 carrots inoculated were experimentally infected with the New York aster-yellows virus. The virus was recovered by means of previously noninfective leafhoppers

from 6 experimentally infected carrots and transferred to 6 healthy asters. The virus was not transferred by previously noninfective leafhoppers from infected carrots to any of the 22 healthy celery plants inoculated. The incubation period of the disease in the plant varied from 15 to 53 days, with an average of 30.9 days.

Three Single or Plain parsley plants (*Petroselinum hortense*) were experimentally infected with the yellows virus from asters infected in New York. The infected parsley plants showed typical symptoms of yellows as described in a previous paper,[13] but the virus was not transferred by leafhoppers from the infected parsley plants to 8 healthy asters and 6 celery plants. The incubation periods of the disease in the plants were 30, 45, and 48 days, respectively, averaging 41 days.

Four Hamburg or Turnip-rooted parsley plants (*Petroselinum hortense radicosum*) were inoculated with the aster yellows virus from New York by means of *Cicadula divisa,* but only 2 plants developed the symptoms of yellows described in a previous paper.[13] The incubation periods of the disease were 40 and 44 days, respectively, averaging 42 days. Previously noninfective leafhoppers, after feeding on the inoculated plants, failed to transmit the disease to 8 healthy asters and 6 celery plants.

An attempt was made to retain the aster yellows virus through the winter in a perennial plant. Infective leafhoppers were transferred from asters infected with yellows from New York to common plantain or ribgrass (*Plantago major*). Large numbers of insects were reared on common plantain; when one lot of plants became unfavorable as food, the insects were transferred to healthy plants. Common plantain was experimentally infected with yellows and showed typical symptoms of the disease, but the virus was not recovered by previously noninfective leafhoppers during the following spring.

Thamnotettix montanus Van D., a newly discovered vector of California aster and celery yellows, failed to transmit yellows from asters infected in New York to any of 71 healthy asters and 10 celery plants. Previously noninfective *Cicadula divisa* after feeding on the 10 celery plants and some of the asters exposed to *Thamnotettix montanus* failed to transmit yellows to healthy asters and celery.

California aster and celery yellows has been transmitted on rare occasions from a feeding solution containing crushed infective *Cicadula divisa* bred on diseased plantain or ribgrass (*Plantago major*). The feeding solution containing the crushed infective leafhoppers was centrifuged at 3,500 r.p.m. for 1 hour and a portion was fed directly to previously noninfective leafhoppers, while the remainder was filtered through coarse and fine Berkefeld candles and the filtrate was fed to previously

noninfective leafhoppers. The methods of feeding the insects were the same as those used with the beet leafhopper and described in previous papers.[12, 16, 17]

Similar experiments were performed with feeding solutions containing crushed infective *Cicadula divisa* which had fed on yellows-infected asters from New York and Wisconsin. Previously noninfective leafhoppers were fed on the centrifuged feeding solutions containing the crushed infective leafhoppers and also on the filtrates. The feeding solutions contained autoclaved filtered root juice from celery, celeriac, carrot, or parsnip plants, or a combination of petiole and root juice from these plants, various proportions of a 2 per cent solution of maltose, and sometimes a 2 per cent solution of soluble starch solution. The same percentage of maltose, or soluble starch, or a combination of both without the plant extract, was also used. The infective leafhoppers were also crushed in sterile distilled water. All efforts to transmit yellows to 130 healthy asters by feeding previously noninfective leafhoppers on centrifuged feeding solutions or on the filtrates failed.

CARROT-YELLOWS VIRUS FROM MAINE

D. Folsom, of the Maine Agricultural Experiment Station, sent ornamental flowering plants, plantain, and carrots naturally infected with yellows, but only the carrots and a species of *Calendula* arrived in good condition.

Experiments were conducted to determine whether the virus could be transmitted by *Cicadula divisa* from carrots infected with yellows in Maine to healthy asters and celery. Previously noninfective leafhoppers after being exposed to carrots naturally infected with yellows obtained from Maine were transferred to 17 healthy asters and 17 healthy celery plants. One typical case of aster yellows developed and one celery plant showed symptoms of yellows, both being transmitted from the same diseased carrot plant. Previously noninfective leafhoppers failed to transmit yellows from the infected celery to several healthy celery plants.

Previously noninfective leafhoppers, after being exposed to yellows-infected carrot plants received from Maine, transmitted yellows to 3 white, 1 yellow, and 7 orange varieties of carrots. Yellows was not transferred by leafhoppers from the experimentally infected carrots to 11 healthy asters and 11 celery plants, as shown in table 3. The incubation period of the disease in the plants varied from 19 to 81 days, with an average of 48.7 days, as indicated in table 3.

Hollow Crown parsnip (*Pastinaca sativa*) was experimentally infected with yellows by previously noninfective leafhoppers which had

been exposed to naturally infected carrots obtained from Maine. The virus was not recovered from infected parsnips by leafhoppers, for they failed to transmit yellows to healthy asters and celery.

Yellows was transmitted by previously noninfective leafhoppers from naturally infected *Calendula sp.* from Maine to healthy asters but not to celery.

TABLE 3

INCUBATION PERIOD OF MAINE CARROT YELLOWS IN EXPERIMENTALLY INFECTED CARROTS AND RECOVERY OF VIRUS BY *Cicadula divisa*

Variety of carrot	Number of plants inoculated	Number of leafhoppers on each plant	Number of plants infected	Number of plants healthy	Incubation period in plant, days	Yellows transferred	
						From carrot to aster	From carrot to celery
Short White	1	55	1	0	54	—	—
White Mastodon	1	50	1	0	54	—	—
White Belgian	1	50	1	0	81	—	—
Yellow Belgian	1	50	1	0	52	—	—
Chantenay	1	50	1	0	45	—	—
Danvers Half Long	1	30	1	0	19	—	—
Early Scarlet Horn	1	50	1	0	54	—	—
French Forcing	1	50	1	0	32	—	—
Long Orange	1	30	1	0	44	—	—
Nantes	1	30	1	0	37	—	—
Oxheart or Guerande	1	30	1	0	44	—	—
Total	11	—	11	0	—	11—	11—
Average	—	43	—	—	48.7	—	—

ASTER-YELLOWS VIRUS FROM INDIANA

Asters infected with yellows were sent by R. W. Samson, of the Purdue University Agricultural Experiment Station, La Fayette, Indiana.

Transmission experiments were conducted with *Cicadula divisa* to determine whether asters, celery, and parsnips could be infected with yellows from diseased asters received from Indiana. Previously noninfective leafhoppers were exposed for a period of 1 or 2 days on asters infected with yellows from Indiana and were then transferred in lots of 10 or 20 to healthy asters and celery. Ten asters were inoculated with yellows and 5 typical cases of aster yellows developed, while 5 plants failed to show symptoms of the disease. Previously noninfective leafhoppers exposed to the 5 infected asters failed to transmit yellows to 5 healthy celery plants. Ten celery plants exposed to infective leafhoppers failed to develop symptoms of celery yellows.

Hollow Crown parsnip was experimentally infected with aster yellows

from Indiana and showed typical symptoms of the disease as described in a previous paper.[13] The virus was not transferred by leafhoppers from infected parsnips to healthy asters and celery.

Common plantain or ribgrass (*Plantago major*) was experimentally infected with yellows during the autumn and showed typical symptoms of the disease, but the virus was not recovered by previously noninfective leafhoppers during the following spring.

ASTER-YELLOWS VIRUS FROM WISCONSIN

Asters naturally infected with yellows were received from A. J. Riker, of the Wisconsin Agricultural Experiment Station, Madison, Wisconsin.

Asters, celery, and parsnip were inoculated by means of *Cicadula divisa* with the virus of aster yellows obtained from Wisconsin. Twenty-six healthy asters were inoculated, and 18 plants developed typical symptoms of aster yellows. Six of the 82 celery plants inoculated showed symptoms of celery yellows. The virus was transferred by previously noninfective leafhoppers from 2 of the 6 celery-yellows plants to asters.

Hollow Crown parsnip was experimentally infected with aster yellows from Wisconsin, but the virus was not transferred by previously noninfective leafhoppers from infected parsnips to healthy asters and celery.

Three white, 1 yellow, and 7 orange varieties of carrots were experimentally infected with yellows from asters naturally infected in Wisconsin. Nineteen of the 22 inoculated carrots showed typical symptoms of carrot yellows as indicated in table 4. Previously noninfective leafhoppers exposed to the inoculated carrots failed to transmit yellows to healthy asters and celery, as shown in table 4. The incubation period of the disease varied from 14 to 44 days, with an average of 29.8 days (table 4).

Male *Thamnotettix montanus* exposed to yellows-infected aster plants from Wisconsin failed to transmit yellows to 18 healthy asters.

CARROT YELLOWS FROM IDAHO

C. F. Henderson,[4] of the United States Department of Agriculture Bureau of Entomology, reported that carrots infected with yellows occurred in Twin Falls, Jerome, and Cassia counties, Idaho, during 1930. He found 17 per cent of the carrots infected with yellows in one field near Twin Falls that year, but during the season of 1932 carrot yellows

[4] Henderson, C. F., letter to author dated November 29, 1932.

was rarely observed in the vicinity of Twin Falls. Henderson sent several shipments of carrots naturally infected with yellows collected near Twin Falls, and the foliage symptoms were identical with carrot yellows in California.

TABLE 4

Incubation Period of Wisconsin Aster Yellows in Experimentally Infected Carrots and Recovery of Virus by *Cicadula divisa*

Variety of carrot	Number of plants inoculated	Number of leafhoppers on each plant	Number of plants infected	Number of plants healthy	Incubation period in plant, days	Yellows transferred	
						From carrot to aster	From carrot to celery
Short White	1	20♂	1	0	29	—	—
	1	20♀	0	1	....	—	—
White Mastodon	1	20♂	1	0	31	—	—
	1	20♀	0	1	....	—	—
White Belgian	1	20♂	1	0	42	—	—
	1	20♀	1	0	23	—	—
Yellow Belgian	1	20♂	1	0	42	—	—
	1	20♀	1	0	28	—	—
Chantenay	1	20♂	1	0	14	—	—
	1	20♀	1	0	28	—	—
Danvers Half Long	1	20♂	1	0	42	—	—
	1	20♀	1	0	28	—	—
Early Scarlet Horn	1	20♂	1	0	22	—	—
	1	20♀	1	0	23	—	—
French Forcing	1	20♂	1	0	18	—	—
	1	20♀	1	0	23	—	—
Long Orange	1	10♂	1	0	30	—	—
	1	10♀	1	0	26	—	—
Nantes	1	20♂	1	0	29	—	—
	1	20♀	1	0	44	—	—
Oxheart or Guerande	1	20♂	1	0	44	—	—
	1	20♀	0	1	....	—	—
Total	22	.....	19	3	....	22—	22—
Average	....	.....	....	....	29 8	.....	.....

Transmission of yellows by previously noninfective *Cicadula divisa* from naturally infected carrots obtained from Idaho to healthy carrots was accomplished with 3 white, 1 yellow, and 5 orange varieties, as shown in table 5. Previously noninfective leafhoppers exposed to the experimentally infected varieties of carrots failed to transmit yellows to

healthy asters and celery. The incubation period of the disease in the plants varied from 24 to 48 days, with an average of 34.2 days, as indicated in table 5.

In another experiment previously noninfective males reared on barley, which is immune to aster yellows, were exposed to carrots naturally

TABLE 5

INCUBATION PERIOD OF IDAHO ASTER YELLOWS IN EXPERIMENTALLY INFECTED CARROTS AND RECOVERY OF VIRUS BY *Cicadula divisa*

Variety of carrot	Number of plants inoculated	Number of leafhoppers on each plant	Number of plants infected	Number of plants healthy	Incubation period in plant, days	Yellows transferred	
						From carrot to aster	From carrot to celery
Short White	1	25 ♀	1	0	24	—	—
White Mastodon	1	10 ♀	1	0	45	—	—
	1	30 ♀	1	0	48	—	—
White Belgian	1	25 ♀	0	1	....	—	—
	1	10 ♀	1	0	41	—	—
Yellow Belgian	1	25 ♀	1	0	31	—	—
Chantenay	1	25 ♀	1	0	27	—	—
French Forcing	1	10 ♀	1	0	43	—	—
	1	20 ♀	1	0	29	—	—
Long Orange	1	25 ♀	0	1	....	—	—
	1	20 ♀	1	0	31	—	—
	1	20 ♀	1	0	29	—	—
	1	20 ♀	1	0	33	—	—
Nantes	1	25 ♀	1	0	32	—	—
Oxheart or Guerande	1	25 ♀	1	0	31	—	—
Total	15	.....	13	2	....	15—	15—
Average	...	.....	....	....	34.2	....	.....

infected with yellows from Idaho and then transferred to healthy asters and celery. In other tests previously noninfective females deposited eggs in the foliage of the diseased carrots, and after nymphs hatched and acquired the winged stage, the males were transferred to healthy asters and celery. Twenty-seven inoculated asters failed to show symptoms of yellows. Sixty-one celery plants were inoculated and 3 of them showed a chlorotic condition of the central leaves with a marked twisting of the petioles. The virus was not recovered from the 3 celery plants showing symptoms of yellows.

CELERY YELLOWS FROM UTAH

In 1927 Linford[7] reported a yellows disease on celery in Salt Lake and Weber counties, Utah. He first observed aster yellows on September 9, 1927, in four localities in Salt Lake and Davis counties, Utah, with a maximum severity of 3 per cent.

Kunkel[6] states, however, that there is no convincing evidence that celery yellows reported in Utah is California yellows.

H. L. Blood, United States Department of Agriculture Bureau of Plant Industry, stationed at the Utah Agricultural Experiment Station, sent 3 small celery-yellows plants from Salt Lake City. Previously noninfective *Cicadula divisa,* after feeding on the celery-yellows plants, transmitted yellows from 2 of the 3 plants to 2 healthy celery plants and 1 aster plant. Unfortunately one of the inoculated aster plants died before symptoms of aster yellows developed. The virus was transferred by previously noninfective *Cicadula divisa* from the 2 experimentally infected celery plants to 2 healthy celery plants. Celery yellows of Utah is probably identical with California aster yellows.

YELLOWS AND CURLY TOP OF ZINNIA

Severin[10] reported that a circular bed of zinnias (*Zinnia elegans*) showing 100 per cent California yellows was found in the center of a lawn in front of the Spreckels Agricultural Experiment Station. *Cicadula divisa* was abundant on the zinnias and on the grass. The plants were stunted, chlorotic, and with abnormal flowers. Noninfective leafhoppers after feeding on the diseased zinnias transmitted yellows to asters and celery.

Kunkel[6] failed to infect *Zinnia elegans* with California yellows experimentally. He was able to infect *Zinnia multiflora* L. with the New York aster-yellows virus, but this species is not grown for seed production in California.

During the summer of 1932, several surveys were made of the yellows and curly-top diseases of ornamental flowering plants grown on seed farms in the San Juan and Salinas valleys. Different varieties and hybrids of *Zinnia elegans* on both seed farms were stunted and showed a yellowing of the apical and secondary shoots. Three varieties of *Zinnia elegans* commonly known as Double Giant Pink, Dahlia Flowered mixed, and Lilliput Scarlet Gem were demonstrated to be naturally infected with yellows. Previously noninfective *Cicadula divisa* after feeding on the 3 varieties of *Zinnia elegans* transmitted yellows to healthy celery.

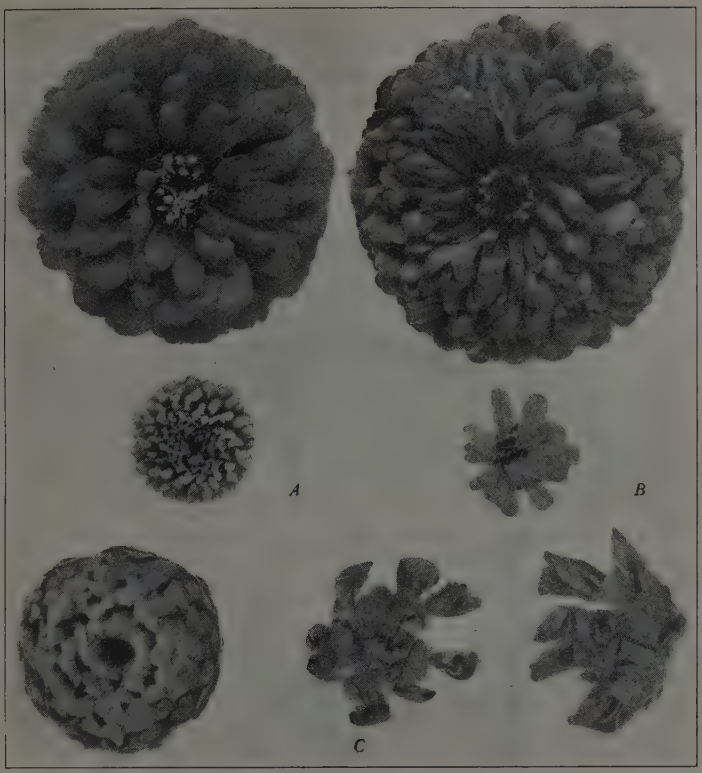

Fig. 1.—*A*, Giant Red zinnia (*Zinnia elegans*): upper, flower from check or control plant; lower, dwarfed flower which was green instead of red in color, from a plant experimentally infected with California aster yellows. *B*, Dahlia Flowered Orange zinnia: upper, flower from check or control plant; lower, dwarfed flower from a plant infected with curly top showing few petals, which were normal in color. *C*, Other abnormal flowers, which were green in color instead of red, from Giant Red zinnia, experimentally infected with California aster yellows.

Previously noninfective beet leafhoppers, *Eutettix tenellus*, after feeding on 9 diseased *Zinnia elegans* transmitted curly top to healthy sugar beets. Four of the 9 zinnias are commonly known as Double Giant type brightness, and were grown adjacent to garden, table, or red beets in the San Juan Valley.

During the summer of 1933 no zinnias infected with yellows or curly top were found on the same seed farms. In the Salinas Valley 40 per cent of the asters were naturally infected with yellows in some plots. Varieties

of zinnias were completely surrounded with diseased asters, but no zinnia yellows was found.

It was decided to attempt experimental infection of different species, varieties, and hybrids of zinnias with California yellows and curly top. Twenty-six Mexican Double Orange zinnias (*Zinnia haageana*) were

Fig. 2.—Giant White zinnia (*Zinnia elegans*) experimentally infected with curly top showing secondary shoots and inward-cupped leaves.

repeatedly inoculated with yellows by lots of 5 or 10 infective *Cicadula divisa*. Three plants developed symptoms of yellows with chlorotic secondary shoots and dwarfed yellow flowers, but the flowers were not abnormal in color. Previously noninfective leafhoppers recovered the virus from the infected plants and transmitted it to healthy asters and celery. No difficulty was experienced in experimentally infecting this species of zinnia with curly top.

Twenty-five varieties or hybrids of *Zinnia elegans* were each inoculated by 2 lots of 10 infective *Cicadula divisa*. Double Pompom White Gem and Giant Red zinnias developed symptoms of yellows, but the virus

was not recovered by previously noninfective leafhoppers. The flowers failed to expand (fig. 1 *A, C*) and were green in color.

The following varieties or hybrids of *Zinnia elegans* were experimentally infected with curly top and the virus was recovered by previously noninfective beet leafhoppers and transferred to sugar beets: Dahlia Flowered Lavender, Dahlia Flowered Orange (fig. 1 *B*) Dahlia Flowered Red, Dahlia Flowered Rose, Double Dahlia Flowered Golden Yellow, Double Dahlia Flowered Light Yellow, Double Dahlia Flowered White, Double Elegans Golden Yellow, Double Elegans Bright Scarlet, Double Elegans Salmon Rose, Double Giant Canary Yellow, Double Lilliput (Dwarf Miniature), Giant Orange, Giant Pink, Giant Purple, Giant Red, Giant White (fig. 2), Double Pompom Dark Crimson, Double Pompom Golden Gem, Double Pompom Salmon Rose, Double Pompom White Gem, Lilliput Crimson Gem, Lilliput Golden Gem, Lilliput Salmon Rose, and Lilliput Pompom Scarlet Gem.[5]

The symptoms of zinnia curly top could not be distinguished from zinnia yellows on old plants in the field, but no study has been made of the symptoms of the two diseases on young plants. Young plants experimentally infected with curly top showed cleared or transparent veinlets, but on old plants infected under natural conditions, this symptom could not be distinguished from normal venation. The internodes near the apices of the branches were shortened with chlorotic secondary shoots arising from the axil of the leaves (fig. 2). The leaves frequently were cupped inward along the midrib. The flowers were dwarfed, with the petals reduced in number but not abnormal in color (fig. 1 *B*).

DISCUSSION

Recovery of Virus.—Kunkel experienced difficulty in the recovery of the aster-yellows virus in New York from experimentally infected host plants. In his first paper Kunkel[4] lists 64 species of plants in 23 families that were experimentally infected with aster yellows, but the virus was transferred back to asters from only 32 species. In a later paper Kunkel[5] reported transmitting yellows to 120 species of plants in 30 families, but the virus was recovered from only 12 species. He states, however, in his second paper that, "while such transmission is necessary in order to bring full proof that the disease observed on any yellowed plant is actually aster yellows, the symptoms are so similar on different hosts that this step was not considered necessary in most cases."

[5] The first seventeen varieties or hybrids were grown from seeds obtained from the Ferry-Morse Seed Co. (1932 catalog) San Francisco, California; the next four from the Germain Seed & Plant Co. (1932 catalog) Los Angeles, California; and the last four from Peter Henderson & Co. (1932 catalog) 35 Cortland St., New York.

The recovery of the aster-yellows virus obtained from other states from host plants showing symptoms of the disease is given in the summary of this paper.

It was sometimes impossible to recover the California aster-yellows virus from naturally infected weeds and experimentally infected economic cultivated plants showing typical symptoms of the disease. Cross inoculations from experimentally infected Double-Curled, Extra-Triple

Fig. 3.—Common buckwheat (*Fagopyrum esculentum*): left, shoot from a plant experimentally infected with California yellows showing large number of flowers with petals which were green in color; right, shoot from a healthy plant used as a check or control showing white flowers.

Curled, and Fern-Leaf or Moss-Curled parsley showing symptoms of yellows were failures, as reported in a previous paper.[13]

Host-Range Differences.—There is some evidence to show that host-range differences occur with California and New York aster yellows. Numerous attempts were made by Kunkel[5] to transmit the aster-yellows virus of New York to potatoes by means of the insect vector. The varieties used included Irish Cobbler, Green Mountain, Bliss Triumph, and Spaulding Rose.

During the past five years, California yellows was transmitted to a number of varieties of potatoes including Bliss Triumph.[14] It was impossible, however, to recover the virus from experimentally infected varieties of potatoes showing symptoms of the disease.

Overlapping Host Ranges.—The overlapping economic host plants of California aster yellows and aster yellows of New York so far investigated are as follows: common buckwheat (*Fagopyrum esculentum*) (fig. 3), spinach (*Spinacia oleracea*), carrot (*Daucus carota* var. *sativa*), dill (*Anethum graveolens*), parsnip (*Pastunaca sativa*), peasant's tobacco (*Nicotiana rustica*) (fig. 4), salsify (*Tragopogon porrifolius*), and lettuce (*Lactuca sativa*). The symptoms of the disease on these over-

Fig. 4.—Peasant's tobacco (*Nicotiana rustica*): *A*, cluster of secondary shoots from a plant experimentally infected with California yellows; *B*, apical shoot from a check or control plant.

lapping host plants infected with the California and New York aster yellows appear to be identical.

It is not to be expected that two different viruses would have identical host ranges. It is not uncommon for two different virus diseases to have overlapping host ranges or to produce similar symptoms.[5] It is difficult to explain, however, why an occasional celery plant developed symptoms of yellows with the aster-yellows virus from other states and the leafhoppers were not able to recover the virus except on very rare occasions. Similar difficulties were encountered with resistant host plants of curly top such as pink beans (*Phaseolus vulgaris*) and Australian saltbush (*Atriplex semibaccata*), as reported in a previous paper.[15]

Smith[18] expressed the opinion that slight differences in the host range do not justify the separation into distinct viruses of entities which are otherwise identical.

Strains of Aster Yellows.—Strains or variants of the aster-yellows viruses transmitted by different species of leafhoppers may occur in the United States, Bermuda Islands,[9] Japan,[3] or Europe.

According to Kunkel,[6] "whether the yellows from California is a strain of aster yellows or is a different disease is a question that cannot be answered at this time." The facts that both are transmitted by the same insect vector, have long incubation periods in the leafhopper, and produce similar symtoms in aster and some other host plants, support the view that they may be related.

According to Smith,[18] "Perhaps the best illustration of two apparently independent strains of a plant virus is afforded by the case of aster yellows and celery yellows. . . . Here then is apparently a case of a virus having 'mutated' or adapted itself to a new host plant in one district and after sojourn in this host [having] acquired the ability to infect it as easily as any other plant in its host range. Such a virus may be regarded merely as a slightly different strain of aster yellows, or it may be regarded as a different entity and be referred to as 'celery yellows.' It is also possible that celery yellows is a stage in the evolution of an entirely new virus."

SUMMARY

Yellows was transmitted by previously noninfective *Cicadula divisa* from asters naturally infected in New York, Indiana, and Wisconsin to asters. Previously noninfective leafhoppers exposed to asters or salsify infected with the disease in New York transmitted yellows to 8 of the 207 celery plants inoculated. The virus was transferred from 1 experimentally infected celery plant to 3 successive healthy asters, but was not transferred from the 3 infected asters back to 12 healthy celery plants. The virus from yellows-infected asters in Wisconsin was transferred to 6 of the 82 celery plants inoculated and from 2 of the 6 experimentally infected celery plants back to asters. Ten celery plants inoculated with the virus of aster yellows from Indiana failed to develop symptoms of the disease.

Yellows was transmitted from celery naturally infected with yellows in Utah to aster and celery plants. The virus was recovered from the experimentally infected celery plants and again transferred to healthy celery plants.

Yellows was readily transmitted to healthy carrots from asters naturally infected with the disease in New York, Maine, and Wisconsin. The transfer of yellows by previously noninfective leafhoppers from experimentally infected carrots to healthy asters was accomplished with 6 of the 22 plants with the aster-yellows virus obtained from New York, but was not performed with 22 healthy celery plants. All efforts to transfer yellows from experimentally infected carrots to healthy asters or celery

with the virus of aster yellows obtained from Maine and Wisconsin failed. No difficulty was experienced in transmitting aster yellows to healthy carrots from carrots naturally infected with the disease in Maine and Idaho. Yellows was transferred from one carrot naturally infected with the disease in Maine to aster and celery, but the virus was not transferred from the infected aster to celery nor from the celery-yellowed plant to any of several healthy celery plants. The transfer of yellows from carrots naturally infected with the disease in Idaho was accomplished with 3 of the 61 celery plants inoculated, but the virus was not recovered from the 3 celery plants showing symptoms of yellows.

Single or Plain parsley, Hamburg or Turnip-rooted parsley, and common plantain or ribgrass (*Plantago major*) were experimentally infected with yellows by previously noninfective leafhoppers which had been exposed to aster yellows obtained from New York, but the virus was not recovered from any of the infected plants. Hollow Crown parsnip was experimentally infected with yellows with the aster-yellows virus from Indiana and Wisconsin and carrot-yellows virus from Maine, but the virus was not recovered from the infected parsnips. The number of tests, however, with all of the species or varieties of plants, was not sufficient to state that the virus could not be recovered on rare occasions.

Thamnotettix montanus Van D., a newly discovered vector of California aster and celery yellows, failed to transmit yellows from asters naturally infected with the disease in New York and Wisconsin to healthy asters and celery.

The results of this investigation show that carrots and asters can be experimentally infected with the aster-yellows virus obtained from New York, Indiana, and Wisconsin, also the carrot-yellows virus from Maine and Idaho, and with the aster-yellows virus from California. Celery was found to be highly resistant to the aster or carrot-yellows virus obtained from all states except California.[10]

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TRANSMISSION OF CALIFORNIA ASTER YELLOWS TO POTATO BY CICADULA DIVISA

HENRY H. P. SEVERIN AND FRANK A. HAASIS

TRANSMISSION OF CALIFORNIA ASTER YELLOWS TO POTATO BY CICADULA DIVISA[1]

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(Contribution from the Division of Entomology and Parasitology, California Agricultural Experiment Station, University of California, coöperating with the United States Department of Agriculture Bureau of Entomology.)

INTRODUCTION

KUNKEL[(1)] FAILED TO TRANSMIT New York aster yellows to potato (*Solanum tuberosum*) by means of the insect vector, *Cicadula divisa* Uhl. [*C. sexnotata* (Fall.)]. The following varieties of potatoes were either immune or highly resistant to the aster-yellows disease: Irish Cobbler, Green Mountain, Bliss Triumph, and Spaulding Rose.

An investigation was undertaken to determine whether potato plants could be experimentally infected with California aster yellows. A study of the symptoms and incubation period of the disease in the plant was made. Attempts were made to recover the virus from infected plants by means of previously noninfective leafhoppers. Trips were made to the potato fields in the delta districts of the San Joaquin Valley to determine whether this virus disease occurs under natural conditions, and observations were made on the relative abundance of the leafhopper on potato plants during the season.

METHODS

The varieties of potatoes used were Bliss Triumph, White Rose, and potatoes grown from seeds. The potatoes were grown in 12-inch flower pots or in large wooden pickle tubs filled with peat soil. The potato plants were enclosed in large cages and inoculated with yellows by 20 to 40 infective leafhoppers. Males were used rather than females so as to avoid egg deposition. The insects inoculated the plants during a period of 1 to 10 days and then the cages containing the males were removed from the plants. The inoculated plants were fumigated with Nico-Fume tobacco-paper insecticide after inoculation and were kept in

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a greenhouse free from leafhoppers or out-of-doors in insect-proof cages. Check or control plants grown from the same tubers were used. Noninfective leafhoppers were kept on some of the control plants, while others were kept free from insects.

RESULTS

During a period of five years, 104 potato plants were inoculated with the California aster-yellows virus by means of infective *Cicadula divisa*, and 50 per cent of the inoculated plants developed symptoms of the disease, as is shown in table 1.

TABLE 1

RESULTS OF INOCULATION OF POTATO PLANTS WITH YELLOWS VIRUS BY CICADULA DIVISA

Dates leafhoppers inoculated plants	Number of potato plants inoculated	Number of leafhoppers on each plant	Number of plants infected	Number of plants healthy	Per cent of plants infected
Sept. 12–15	14	25	14	0	100 0
Sept. 18–23	13	20	13	0	100.0
Oct. 8– 9	12	30	7	5	59 3
Oct. 9–11	11	30	1	10	9.0
Oct. 16–17	8	25	4	4	50.0
Oct. 17–18	8	25	0	8	0.0
Oct. 30–Nov. 2	5	25	2	3	40.0
Feb. 1– 4	1	40	0	1	0.0
Feb. 11–21	2	40	0	2	0.0
Feb. 21–28	1	40	1	0	100 0
Mar. 10–19	1	40	0	1	0.0
Apr. 12–May 9*	1	20	0	1	0.0
Apr. 15–May 9*	2	20	0	2	0.0
Apr. 18–May 9*	2	20	0	2	0.0
Apr. 26–May 13*	4	20	2	2	50.0
June 5–18	4	25	2	2	50.0
June 9–18	5	25	3	2	60.0
June 11–18*	4	35	1	3	25.0
June 11–18	5	35	1	4	20.0
July 7 –18	1	25	1	0	100.0
Total or percentage	104	....	52	52	50.0

* Potato plants grown from seeds.

Symptoms.—The most pronounced symptoms which appeared on potato plants infected with the California aster-yellows virus were purple slender sprouts (figs. 1*A*, 2*A*, *B*, 3 *C–M*) and purple sessile aerial tubers[4] (figs. 1*B*, 4) which developed from the axils of the leaves. Sometimes aerial tubers developed at the end of the sprouts (figs. 1*A*, 3*B*). Fre-

[4] Richard and Blood[2] described and figured aerial tubers in their contribution on psyllid yellows of the potato. H. L. Blood, E. S. Schultz, and M. Shapovalov have examined potato plants showing symptoms of California aster yellows, and all agreed that the symptoms were not identical with those of psyllid yellows.

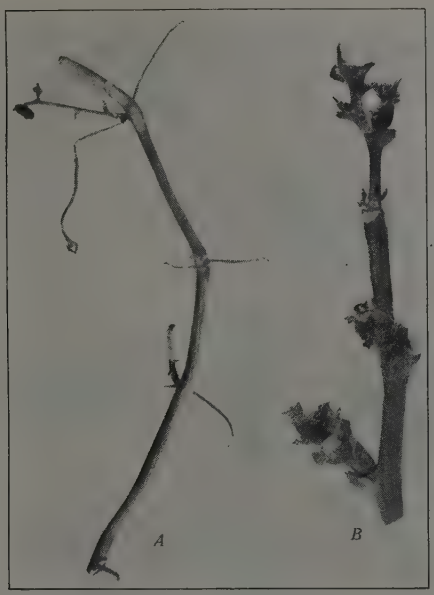

Fig. 1.—Stems of potato plant infected with yellows with leaves removed: *A*, slender sprouts; *B*, sessile aerial tubers growing from buds at the nodes.

Fig. 2.—*A*, *B*, Shoots from potato plant infected with yellows showing slender sprouts growing from the axils of the leaves; *C*, shoot from check or control plant from the same tuber.

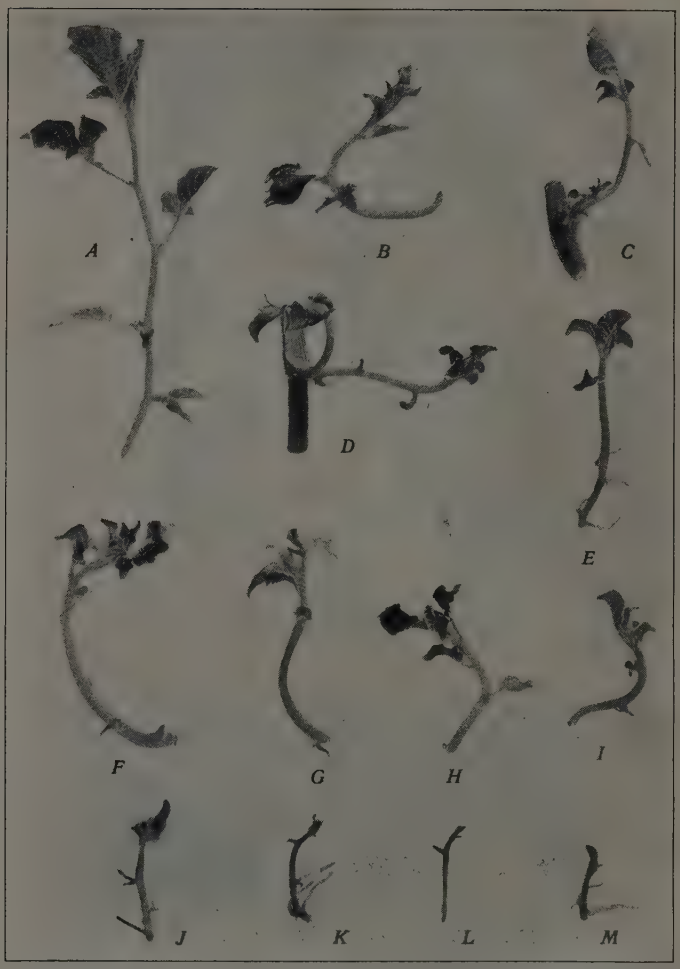

Fig. 3.—Axillary shoots from potato plants grown from seeds infected with yellows: *A*, normal leaves; *B*, aerial tuber; *C–I*, curved petioles with terminal leaflets and lateral sprouts; *J–M*, petioles with lateral sprouts which may represent the veins of undeveloped leaves.

quently dwarfed leaves developed on the aerial tubers (fig. 1*B*). The margins of the leaves were rolled inward (figs. 2*A*, *B*) with the petioles often bent or curved downward (fig. 4). The leaves and stems were brittle. In the later stages of the disease the lower leaves turned yellow and became dry (fig. 4).

Fig. 4.—Shoot from potato plant infected with yellows showing sessile tubers growing from the axils of the leaves, and dried lower leaf.

Potato plants grown from seeds were infected with yellows and the symptoms of the disease were studied. The internodes were shortened and secondary shoots with or without leaves developed from the axils of the leaves (fig. 3*B–J*). The secondary shoots frequently developed purple, slender, lateral sprouts, which may represent veins of leaflets which failed to develop (fig. 3*C–M*) as in the case of shoe-string mosaic of tomatoes. Purple aerial tubers sometimes grew on the secondary shoots (fig. 3*B*).

Incubation Period of Disease in the Plant.—The length of time that elapsed from the inoculation of the potato plants until slender sprouts or aerial tubers developed in the axils of the leaves was considered as the incubation period of the disease and varied as follows: autumn 20 to 37 days; late winter and early spring 50 to 63 days; and summer 27 to 40 days.

Recovery of Virus.—All attempts to recover the virus from potato plants which developed symptoms of yellows disease were failures. Noninfective leafhoppers were fed on all of the infected potato plants and were transferred to healthy asters and celery but not a single case of aster or celery yellows developed. Noninfective leafhoppers failed to recover the virus by feeding on the cut surfaces of potato tubers obtained from plants which had shown symptoms of the yellows. No experiments have been conducted up to the present time on transmitting yellows from infected to healthy potato plants by grafting or budding.

Controls.—Plants grown from cuttings of each tuber and potato plants grown from seeds were used as checks or controls. Noninfective leafhoppers were fed on some controls, others were kept free from insects. All controls remained healthy.

Under Natural Conditions.—Potato plants infected with yellows have not been found under natural conditions up to the present time. *Cicadula divisa,* however, was taken in small numbers in the potato fields in the delta districts of the San Joaquin Valley, throughout the growing season in 1930–1932, but the beet leafhopper, *Eutettix tenellus* (Baker) was more abundant, especially during 1932.

SUMMARY

Fifty per cent of the potato plants inoculated with California aster yellows developed symptoms of the disease. The most pronounced symptoms of the disease were purple slender sprouts and aerial tubers arising from the axil of the leaves. The incubation period of the disease varied from 20 to 63 days during the four seasons. The virus was not recovered from infected potato plants nor from potato tubers obtained from plants showing symptoms of yellows. The disease has not been found in potato fields under natural conditions up to the present time, but *Cicadula divisa* was taken in potato fields.

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TRANSMISSION OF CALIFORNIA ASTER AND CELERY-YELLOWS VIRUS BY THREE SPECIES OF LEAFHOPPERS

HENRY H. P. SEVERIN

TRANSMISSION OF CALIFORNIA ASTER AND CELERY-YELLOWS VIRUS BY THREE SPECIES OF LEAFHOPPERS[1]

HENRY H. P. SEVERIN[2]

(Contribution from the Division of Entomology and Parasitology, California Agricultural Experiment Station, University of California, coöperating with the United States Department of Agriculture, Bureau of Entomology.)

INTRODUCTION

IT HAS BEEN SUGGESTED that possibly an obligate relation exists between a specific insect vector and the aster-yellows virus, and that developmental changes and multiplication of the virus take place during the incubation period in the insect.[8] It has been assumed in the past that the aster-yellows virus could be disseminated only by the leafhopper, *Cicadula divisa* Uhl., which is widely distributed in America.

Ogilvie[10] reported yellows of China aster (*Callistephus chinensis*) in Bermuda, where *Cicadula sexnotata* (Fall.), responsible for the transmission of the virus there, has been known to occur since 1924. The disease also occurs on cos lettuce, cabbage lettuce, eight species of ornamental flowering plants, and several wild plants in Bermuda.

Fukuski[5] reported that aster yellows occurs in Japan. Kunkel[8] reported that *Cicadula sexnotata* occurs in Japan and probably throughout the Orient.

Dobroscky[3] reported that aster yellows was found in the gardens of the Budapest Experiment Station, and in the vicinity of Lake Balaton Biological Laboratory, Hungary. *Cicadula sexnotata* is widespread and common in Europe.[8]

In California three species of leafhoppers transmit the aster-yellows virus. *Cicadula divisa* transmits the virus with greater efficiency than the mountain leafhopper, *Thamnotettix montanus* Van D. or the geminate leafhopper, *T. geminatus* Van D. Experiments with the leafhoppers *Agallia californicum* (Baker), *A. cinera* (O. & B.), and *Empoasca abrupta* De L. bred on celery failed to transmit the yellows virus.[13]

An investigation was undertaken to determine whether or not California aster and celery yellows are caused by two viruses or a single

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virus, and whether the viruses could be separated by the three vectors. Transmission experiments with yellows by the three species of leafhoppers were conducted with the virus obtained from naturally infected asters, celery, and carrots, and from these same host plants experimentally infected by the different species of leafhoppers. Attempts were made to recover the virus from these experimentally infected host plants with the three species of previously noninfective leafhoppers. The host range of the disease among economic plants and weeds was also investigated. The characteristics, distribution, and food plants of two newly discovered vectors of California yellows are discussed in this paper.

METHODS

One method used in the separation of a mixture of viruses in the living plant is by the selective transmission of one virus by the insect vector. Hoggan[7] has shown that the peach aphid, *Myzus persicae* Sulz., transmits only the cucumber mosaic virus from a combination of cucumber and tobacco mosaic viruses, although the tobacco virus was present in the leaves upon which the aphids had fed. Bennett[3] demonstrated that *Aphis rubiphila* Patch transmitted only the curl virus of raspberries and *Amphorophora rubi* Kalt transmitted only the yellow mosaic virus and a medium type of mosaic from a raspberry infected with the three diseases. Smith[16] utilized the peach aphid, *Myzus persicae,* in the separation of potato viruses.

The method adopted to determine whether California aster yellows and celery yellows are caused by two viruses or a single virus was to conduct transmission experiments with yellows by the three species of leafhoppers from naturally and experimentally infected asters, celery, and carrots to healthy plants grown from seeds. It was found that *Cicadula divisa* occurred on all of these host plants in the field. *Thamnotettix montanus* was rare on asters, abundant on celery, and common on carrots. *T. geminatus* was often collected on asters, rarely on celery, and commonly on carrots. These three host plants were transplanted in pots in the greenhouse and healthy plants grown from seeds were used as checks or controls.

Production of Noninfective Leafhoppers.—The production of noninfective *Cicadula divisa* on Sacramento barley immune to the yellows disease has been described in a previous paper.[13] The production of noninfective *Thamnotettix montanus* and *T. geminatus* on barley failed because these species of leafhoppers did not complete their life cycles on that plant. The method adopted was similar to that used with the beet leafhopper, *Eutettix tenellus* (Baker), described in a previous paper.[12]

Several hundred females of each species oviposited in large celery plants for a period of one week and were then removed. Nymphs were transferred after emergence from the egg, before they had an opportunity to feed, from diseased to healthy celery plants, with a fine camel's-hair brush moistened at the tip. The leafhoppers reared to the adult stage on healthy celery, as well as later generations so bred, failed to produce the disease.

DETERMINATION OF THE SPECIES

Thamnotettix Montanus.—The mountain leafhopper, *Thamnotettix montanus*, is 4.5 to 6.0 mm long, with white or yellowish face, a transverse brownish band between the eyes, a conspicuous yellow transverse band on the pronotum, and the scutellum brown (pl. 1, *C, D, E, F*). The summer adults collected in the northern San Joaquin, southern Sacramento, Santa Clara, and Salinas valleys were dark brown (pl. 1, *C, D*) while the specimens taken during the autumn were usually black (pl. 1, *E, F*), with intermediates between the two color patterns.

Thamnotettix montanus has been recorded from British Columbia,[19] Washington,[22, 23] Oregon,[22] California, [20, 22] Nevada,[4] Idaho,[4] and Colorado[6, 19] and probably occurs in most of the western states.

Essig[4] reported that *Thamnotettix montanus* is common on grasses, weeds, carrot, larkspur, goldenrod, apple, and prune.

This leafhopper has a wide range of food plants in California. Adults were collected abundantly on celery growing in the Sacramento Valley, but not so abundantly in the fog belt of the Santa Clara and Salinas valleys. Adults were commonly taken and an occasional nymph on White Icicle radish and Purple Top White Globe turnip in the delta districts near Stockton, in the San Joaquin Valley. The leafhopper was rarely taken on asters in the Salinas Valley. The insects were occasionally captured on the following economic plants in the Sacramento and San Joaquin valleys:

Chenopodiaceae: sugar beets, garden, red, or table beets.
Leguminosae: alfalfa and beans.
Cucurbitaceae: squash, pumpkin, and cucumbers.
Solanaceae: potatoes.
Cruciferae: Chinese cabbage.
Umbelliferae: carrots.
Compositae: lettuce.

Weeds as food and breeding plants of *Thamnotettix montanus* have received little attention up to the present time. The adults were taken

[4] Several shipments of *Thamnotettix montanus* were received from Twin Falls, Idaho, collected by C. F. Henderson.

in small numbers on tumbleweed (*Amaranthus graecizans*). Nymphs hatched from eggs deposited in curly dock (*Rumex crispus*) under natural conditions and were reared to the adult stage on this host plant.

Thamnotettix Reductus.—Van Duzee[5] determined the species from California and Idaho as *Thamnotettix reductus,* and "considers *reductus* as a species distinct from *montanus,* although it was described as a variety."[(22)] De Long[6] could find no genital character which is constant and distinctive on the adults from California and Idaho, but in certain groups it is very difficult to find characters on the genitalia. He states, "I do not feel, however, that *reductus* is a distinct species."

Since *Thamnotettix montanus* and *T. reductus* are considered distinct species on the basis of color pattern only and since there is a difference of opinion among systematists as to the species, the name used in this paper is *montanus.* The description of *T. montanus reductus* by Van Duzee[(22)] follows:

> This form seems to be purely a color variety in which the yellow saddle is reduced to a small mark on the apex of the claval nervures, often on the outer nervures only, or in a few dark males it may be entirely wanting. The brown band on the base of the vertex is also reduced, sometimes to a mere shade, but there may be a dark line next the eye and a geminate spot on the basal middle. Both forms are found together throughout their range, but the present form is much more abundant toward the south, while those from Oregon and Washington are almost entirely typical *montanus.*

Specimens of *Thamnotettix* received from C. F. Henderson, Twin Falls, Idaho, were determined as *T. reductus* by Van Duzee and as *T. montanus* by De Long. The leafhoppers from Idaho transmitted yellows to healthy celery but not to asters. The virus was recovered and transferred by previously noninfective *Cicadula divisa* from the celery infected with yellows by the *Thamnotettix* from Idaho to healthy asters and celery.

Thamnotettix Geminatus.—The geminate leafhopper, *Thamnotettix geminatus,* is 5 to 6 mm long, greenish yellow or brown, with a pair of black spots on the anterior border of the head, a black spot on each side of the eye, an arched band near the front border of the pronotum, and black spots on the scutellum (pl. 1, *G, H*). A more detailed description of the species is given by Van Duzee.[(19)]

Thamnotettix geminatus has been recorded from Colorado,[(6, 18)] Idaho,[7] California,[(20, 22, 23)] Washington,[(11)] and Alaska.[(1)] It has been recorded under the name *Cicadula laeta* from Alaska and Shumagin and

[5] Van Duzee, E. P., letter to author dated November 25, 1930.

[6] DeLong, D. W., letter to author dated August 15, 1932.

[7] Several shipments of *Thamnotettix geminatus* were received from Twin Falls, Idaho, collected by C. F. Henderson.

Popof islands by Ashmead.[1] One specimen under the same name also is in the United States National Museum from Unga Island.[1]

Osborn[11] reported that *Thamnotettix geminatus* occurred in such numbers upon clover, alfalfa, and timothy in the state of Washington, especially at Pullman, as to threaten to become destructive. Additional food plants recorded by Essig[4] include grasses, grains, and apple. Van Duzee[20] found the leafhopper common on *Malvastrum* in San Diego County, California

No intensive study has been made of the food and breeding plants of *Thamnotettix geminatus* in California. The adults were commonly taken on carrots in the Sacramento and Salinas valleys, but rarely on celery, and often on asters in the Salinas Valley.

TRANSMISSION OF YELLOWS BY THAMNOTETTIX MONTANUS TO HEALTHY ASTERS AND CELERY

Collected on Celery Under Natural Conditions.—During 1931 a serious outbreak of celery yellows occurred in the Sacramento and Santa Clara valleys, and celery in many fields was plowed under. *Thamnotettix montanus* was very abundant in the celery fields near Sacramento. Adults captured in the celery fields transmitted yellows to 2 of 12 healthy celery plants but not to asters, as shown in table 3 (p. 348). These results demonstrate that this insect is a vector of celery yellows under natural conditions.

Fed on Naturally Infected Asters and Celery.—A comparison was made of the transmission of yellows by previously noninfective *Cicadula divisa* and *Thamnotettix montanus* from 10 asters naturally infected with the disease to healthy asters and celery. Ten lots, each consisting of 10 *C. divisa* or 10 *T. montanus* were fed for a period of 2 days on 10 diseased asters, one lot to a plant, and then each lot was fed for a period of 21 days on a healthy aster or celery plant; *T. montanus* was used only on celery. Each lot was then transferred to successive healthy aster or celery plants and was kept on each plant for a period of 10 days. In the recovery of the virus from celery experimentally infected by *T. montanus* with the virus from naturally infected asters, the feeding period on the infected celery plants varied from 4 to 33 days. The results obtained are indicated in table 1.

The results in table 1 show that previously noninfective *Cicadula divisa* after feeding 2 days on asters naturally infected with yellows transferred the virus to 45 per cent of the healthy asters and to 48.3 per cent of the healthy celery plants. Previously noninfective *Thamnotettix mon-*

tanus after feeding 2 days on asters naturally infected with yellows transferred the virus to 20 per cent of the healthy celery plants as shown in table 3, and recovered the virus from 3 of the 4 celery plants which they had infected (table 1), or 75 per cent.

Tests were made on the transmission of yellows by *Thamnotettix montanus* from naturally infected celery. Seventeen lots of 10 or 20 *T. mon-*

TABLE 1

Comparison of Transmission of Yellows by Previously Noninfective Cicadula Divisa and Thamnotettix Montanus from Naturally Infected Asters to Successive Healthy Asters and Celery, and Recovery of Virus by T. Montanus*

Source of inoculation: aster-yellows plant no.	Successive aster and celery plants inoculated							Virus recovered from celery infected by *T. montanus* and transferred by this leafhopper to celery	
	By *C. divisa*					By *T. montanus*			
	Asters		Celery			Celery			
	First set	Second set	First set	Second set	Third set	First set	Second set	First set	Second set
1	+	+	+	+	+	−	−		
2	+	+	+	+		−	+	+	−
3	−	−	−	−	−	−	−		
4	−	−	−	−	−	−	−		
5	+	+	+	+	−	−	+	−	+
6	−	−	−	−	−	−	−		
7	−	−	−	−	−	−	−		
8	+	+	+	−	−	−	+	−	−
9	+	+	+	+	+	−	+	−	+
10	−	−	+	+	+	−	−		
Total +	4+	5+	6+	5+	3+	0+	4+	1+	2+
Total −	6−	5−	4−	5−	6−	10−	6−	3−	2−

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted.

tanus each were fed for a period of 3 weeks on diseased celery plants. Each lot was then transferred at weekly intervals to 3 successive healthy celery plants and to 1 aster. A comparison was also made of the recovery of the virus by previously noninfective *T. montanus* and *Cicadula divisa* from celery experimentally infected with yellows by *T. montanus*. The same procedure was used in the recovery of the virus from experimentally infected celery with the two insects except that with *T. montanus* 2 successive healthy celery and 1 aster plants were used, and with *C. divisa* 1 healthy celery and 1 aster. Table 2 indicates the results obtained.

The percentage of transmission of yellows by *Thamnotettix montanus* to successive healthy celery and aster plants and the recovery of the virus by the same species of leafhopper and by *Cicadula divisa* from experi-

mentally infected celery to healthy celery and asters is given in table 2 and summarized in table 3. With 3 successive sets of celery plants, 9 of the 51 inoculated, or 17.6 per cent, and with 1 set of asters 2 of the 17 plants inoculated, or 11.8 per cent, were infected with yellows by *T. montanus* that had fed on naturally infected celery plants (table 3). From experimentally infected plants, the virus was recovered by *T. montanus* and transferred to celery from 5 of the 9 infected celery plants, or 44.4 per cent, but was not transferred to any of 9 asters inoculated; it was recovered by *C. divisa* from all of the 9 infected celery plants and transferred to all of the 9 celery and 9 aster plants inoculated, or 100 per cent (table 2).

TABLE 2

TRANSMISSION OF YELLOWS BY THAMNOTETTIX MONTANUS FROM NATURALLY INFECTED CELERY TO SUCCESSIVE HEALTHY CELERY AND ASTERS AND RECOVERY OF VIRUS FROM EXPERIMENTALLY INFECTED PLANTS BY T. MONTANUS AND CICADULA DIVISA*

Number of *T. montanus* transferred from infected celery	Successive celery and aster plants inoculated by *T. montanus*				Virus recovered from experimentally infected celery and transferred				
					By *T. montanus*			By *C. divisa*	
	Celery			Aster	To celery		To aster		
	First set	Second set	Third set		First set	Second set		To celery	To aster
10	−	+	+	−	++	++	−−	++	++
10	−	+	−	−	−	−	−	+	+
20	+	−	−	−	+	+	−	+	+
20	+	−	−	+	−	−	−	+	+
20	+	−	−	+	+	−	−	+	+
20	−	+	−	−	+	−	−	+	+
20	−	+	−	−	−	−	−	+	+
20	−	−	+	−	−	−	−	+	+
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−		....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
Total +	3+	4+	2+	2+	5+	3+	0+	9+	9+
Total −	14−	13−	15−	15−	4−	6−	8−	0−	0−
Percentage	*17.6*	*23.5*	*11.8*	*11.8*	*55.5*	*33.3*	*0.0*	*100*	*100*

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted. ++ = Virus recovered from 2 sets of experimentally infected celery. −− = Failure to recover virus from 2 sets of plants tested.

In another experiment to test transmission by *Thamnotettix montanus* to asters, each lot of 5 or 10 adults of *T. montanus,* after feeding for a period of 3 weeks on celery naturally infected with yellows, was transferred to healthy asters. Four of 15 aster plants inoculated, or 26.6 per cent, were infected with yellows, as shown in table 3. The virus was not recovered from the 4 experimentally infected asters by *T. montanus,* but was recovered by *Cicadula divisa* and transferred to healthy asters and celery.

Bred on Naturally Infected Asters and Celery.—Aster was an unfavorable food plant for the adults of *Thamnotettix montanus,* but the nymphs often acquired the winged stage on large aster plants. Lots of 10, 20, or 25 adults bred on asters naturally infected with yellows were transferred to one or more healthy celery plants and then to healthy asters. Thirty-two celery plants were thus inoculated, and 8, or 25 per cent, became diseased as indicated in table 3. Twenty-two asters were inoculated by the same lots of leafhoppers, but not a single case of aster yellows developed (table 3).

Fifty lots of 20 *Thamnotettix montanus* which had completed the nymphal stages on celery naturally infected with yellows were transferred to healthy celery, one lot to each plant. Fifteen of 50 celery plants thus inoculated, or 30 per cent, developed the disease (table 3).

Fed on Asters and Celery Experimentally Infected by Thamnotettix Montanus.—Nymphs were fed on asters experimentally infected with yellows by *Thamnotettix montanus* and after they acquired the winged stage, each of 25 lots of 5 adults were transferred to a healthy aster, but again all of the plants remained healthy (table 3).

An attempt was made to transfer the virus from asters experimentally infected with yellows by *Thamnotettix montanus* to healthy celery by lots of 50 or 100 males. Each lot of leafhoppers was fed on diseased asters and healthy celery, alternating daily, until all of the insects were dead. With this method the leafhoppers lived from 21 to 42 days. All of the four celery plants inoculated by this method failed to develop the disease (table 3).

Fifteen lots of *Thamnotettix montanus* were fed for a period of 3 weeks or longer on celery experimentally infected by this leafhopper and then each lot was transferred to a healthy aster. One of the 15 asters inoculated, or 6.6 per cent, developed the disease (table 3).

Males of *Thamnotettix montanus* were fed for a period of 3 weeks or longer on 18 celery plants experimentally infected with yellows by *T. montanus* and then each lot of 20 males was transferred to 1 or 2 healthy celery plants. Thirty-four of 70 lots transmitted yellows to 34 of 96 cel-

ery plants inoculated, or 35.4 per cent (table 3). The virus was transferred by *Cicadula divisa* from the original celery plants infected with yellows by *Thamnotettix montanus,* to 14 of the 18 healthy asters inoculated, or 77.7 per cent.

Fed on Asters and Celery Experimentally Infected by Cicadula Divisa.—Thamnotettix montanus, after feeding on asters experimentally infected with yellows by *Cicadula divisa,* were transferred to 104 healthy asters, but only 2 asters, or 1.9 per cent, became diseased (table 3). A high mortality of the leafhoppers occurred on small asters, and in all probability the incubation period of the virus in many of the insects was not completed.

Thamnotettix montanus, after feeding on asters infected with yellows by *Cicadula divisa,* were transferred in lots of 20 specimens to 1 or 2 healthy celery plants. Seven of the 39 celery plants inoculated, or 17.9 per cent, became diseased (table 3).

Since a high mortality of the adults occurred on asters, it was decided to feed the leafhoppers for periods varying from 3 to 5 weeks on celery experimentally infected with yellows by *Cicadula divisa.* In one experiment each lot of 5 adults was transferred to 1 or 2 healthy asters and they remained on the plants until all were dead. With twenty-nine lots of 5 insects each, 49 asters were inoculated, but no yellows developed (table 3). In a second experiment lots of 20 leafhoppers were used to inoculate 124 asters, and 3 plants, or 2.4 per cent, developed symptoms of yellows (table 3). Previously noninfective *C. divisa* transferred the virus from the 3 infected asters to healthy asters and celery, but *Thamnotettix montanus* failed to recover the virus. In a third experiment 4 lots of 100 *T. montanus,* after feeding for a period of 27 days on celery experimentally infected with yellows by *C. divisa,* failed to transmit the virus to 4 healthy asters (table 3). In a fourth experiment repeated inoculations of each of 6 healthy aster plants were made by lots of 20 male *Thamnotettix montanus* which had fed for periods varying from 26 to 57 days on celery experimentally infected with yellows by *Cicadula divisa;* when one lot of 20 leafhoppers died on an aster another lot of 20 specimens was put in the cage enclosing the plant, and so on until 5 successive lots of 20 insects were used on each plant. Three lots of 20 males were dead at the end of 1 day on small asters while 1 specimen of another lot lived 18 days. The average longevity of the last living male with 30 lots of 20 leafhoppers was 5 days on small asters. The six asters inoculated by this method remained healthy (table 3).

Lots of 20 *Thamnotettix montanus* were fed for a period of 3 weeks or longer on celery infected by *Cicadula divisa* and then each lot was trans-

ferred to 1 or 2 healthy celery plants. Thirty-six of the 134 celery plants inoculated, or 26.9 per cent, developed symptoms of yellows (table 3).

Fed on Celery Experimentally Infected by Thamnotettix Geminatus.—*Thamnotettix montanus* transmitted yellows from celery experimentally infected by *T. geminatus* to 6 of 26 healthy celery plants inoculated,

TABLE 3

Summary of Results on Transmission of Yellows by Thamnotettix Montanus to Healthy Asters and Celery

Source of virus	Asters inoculated	Asters infected	Asters healthy	Per cent infected
Collected on celery under natural conditions	12	0	12	0.0
Fed on naturally infected celery	17	2	15	11.8
Fed on naturally infected celery	15	4	11	26.6
Bred on naturally infected asters	22	0	22	0.0
Fed on asters experimentally infected by *T. montanus*	25	0	25	0.0
Fed on celery experimentally infected by *T. montanus*	15	1	14	6.6
Fed on asters experimentally infected by *Cicadula divisa*	104	2	102	1.9
Fed on celery experimentally infected by *C. divisa*	49	0	49	0.0
	124	3	121	2.4
	4	0	4	0.0
	6	0	6	0.0
Fed on celery experimentally infected by *T. geminatus*	19	0	19	0.0
Total	412	12	400	.....
Percentage	.....	....	.....	*2.9*

Source of virus	Celery inoculated	Celery infected	Celery healthy	Per cent infected
Collected on celery under natural conditions	12	2	10	16.7
Fed on naturally infected asters	20	4	16	20.0
Fed on naturally infected celery	51	9	42	17.6
Bred on naturally infected asters	32	8	24	25.0
Bred on naturally infected celery	50	15	35	30.0
Fed on asters experimentally infected by *T. montanus*	4	0	4	0.0
Fed on celery experimentally infected by *T. montanus*	96	34	62	35.4
Fed on asters experimentally infected by *C. divisa*	39	7	32	17.9
Fed on celery experimentally infected by *C. divisa*	134	36	98	26.9
Fed on celery experimentally infected by *T. geminatus*	26	6	20	23.1
Total	464	121	343	.....
Percentage	.....	.....	.....	*26.1*

or 23.1 per cent, but failed to transmit the virus to any of 19 healthy asters inoculated (table 3). The virus was not recovered from the 6 celery plants by *T. montanus* but was recovered by previously noninfective *Cicadula divisa* and transferred to healthy aster and celery.

The transmission of yellows from all sources by *T. montanus* to asters average 2.9 per cent and to celery 26.1 per cent as summarized in table 3.

TRANSMISSION EXPERIMENTS WITH SUGAR-BEET CURLY TOP

Since the beet leafhopper, *Eutettix tenellus* (Baker), the vector of sugar-beet curly top in North America, is closely related to the genus, *Thamnotettix,* (it was originally placed in the latter genus [2, 6]) tests were made on whether or not *T. montanus* could transmit sugar-beet curly top. Previously noninfective nymphs or adults, after feeding on curly-top beets, were transferred to 24 healthy beet seedlings, but no curly top developed. Since a high mortality of the leafhoppers occurred on sugar beets, 5 lots of 100 males were fed alternating daily on curly-top beets and healthy celery for a period varying from 1 to 2 weeks, and then each lot of leafhoppers was kept on a healthy beet until the last specimen died. The five beets remained healthy.

ADDITIONAL HOST PLANTS EXPERIMENTALLY INFECTED WITH YELLOWS BY THAMNOTETTIX MONTANUS

Carrot Yellows.—Thamnotettix montanus was collected on carrots (*Daucus carota* var. *sativa*) in the Salinas, San Juan, and Sacramento valleys. Previously noninfective leafhoppers, after feeding on 5 carrots naturally infected with yellows, were transferred to 10 healthy celery plants, and 4 of these developed symptoms of yellows. The virus was transferred by previously noninfective *T. montanus* from 2 of these 4 experimentally infected celery plants to healthy celery plants, but attempts to transfer it to asters and carrots were unsuccessful.

An attempt was made to experimentally infect with yellows from celery by means of *Thamnotettix montanus* 3 white, 1 yellow, and 7 orange varieties of carrots. Two plants of each variety were repeatedly inoculated by different lots of leafhoppers. Oxheart or Guerande, an orange variety of carrot, developed typical symptoms of the disease similar to those on carrots infected by *Cicadula divisa* described in a previous paper.[13] The virus was transferred by previously noninfective *C. divisa* from the carrot experimentally infected with yellows to healthy aster and celery plants, but *T. montanus* failed to recover the virus from the carrot.

White London Mustard Yellows.—White London mustard (*Brassica alba*) is a new host plant of aster yellows. This mustard was experimentally infected with yellows by both *Thamnotettix montanus* (in 1 of 2 tests made) and *Cicadula divisa* from the mustard plants experimentally

infected with yellows to healthy asters and celery, but *T. montanus* failed to recover the virus from mustard.

Plants infected with yellows by the two species of leafhoppers developed similar symptoms. The apical leaves were dwarfed, cupped out-

Fig. 1.—White London mustard (*Brassica alba*) experimentally infected with yellows by *Thamnotettix montanus*, showing dwarfed, outward-cupped apical leaves and secondary shoots arising from the axils of the older leaves.

ward, and yellow. Secondary shoots developed from the axils of the leaves (fig. 1).

Prickly Winter Spinach Yellows.—Prickly Winter spinach (*Spinacia oleracea*) was experimentally infected with yellows by *Thamnotettix montanus* (in 1 of 10 tests made) and *Cicadula divisa*. The virus was transferred by previously noninfective *T. montanus* from experimen-

tally infected spinach to healthy celery but not to asters, and by *C. divisa* to both celery and asters.

The symptoms of the disease on spinach infected with yellows by the two species of leafhoppers were similar. The petioles of the outer leaves

Fig. 2.—Prickly Winter spinach (*Spinacia oleracea*) infected with yellows by *Thamnotettix montanus* showing elongated petioles of the outer leaves and many upright secondary shoots with dwarfed leaves and shortened petioles.

were elongated, and many upright secondary shoots developed with dwarfed leaves and shortened petioles (fig. 2).

Prizehead Lettuce Yellows.—Lettuce (*Lactuca sativa*) of the variety Prizehead was experimentally infected with yellows from celery by *Thamnotettix montanus* (only 1 test was made) and developed symptoms of the disease similar to those on lettuce infected by *Cicadula divisa* as described in a previous paper.[13] The virus was transferred by previously noninfective *C. divisa* from experimentally infected lettuce to asters and celery, but *T. montanus* failed to recover the virus from lettuce.

Plantain or Ribgrass Yellows.—In a previous paper[13] plantain or ribgrass (*Plantago major*) was reported to be naturally infected with yellows. Tests were made to determine whether plantain could be experimentally infected with yellows from celery by *Thamnotettix montanus* and whether the leafhopper could recover the virus from infected plantain and transfer it to asters. Previously noninfective *T. montanus* were fed for a period of 36 days on celery experimentally infected with yellows by *Cicadula divisa.* Lots of 20 *T. montanus* were transferred from the celery-yellows plants to 4 healthy plantain plants, and one plant developed typical symptoms of yellows after an incubation period of the disease of 54 days. Seven lots of 5, and 12 lots of 20 *T. montanus* per plant, all failed to transmit the virus from the experimentally infected plantain to 19 healthy asters. On the other hand, previously noninfective *C. divisa* transmitted the virus from experimentally infected plantain to healthy asters..

Tests were also made to determine whether *Thamnotettix montanus* could recover the virus from plantain experimentally infected with yellows by *Cicadula divisa* which had fed on asters or celery naturally infected with the disease. Nymphs of *T. montanus* were fed on diseased plantain until the insects acquired the winged stage and then 10 or 20 males were transferred to healthy asters and celery plants. Often the males were used to inoculate one or more healthy celery plants and then were transferred to one or several asters. Thirty-five asters and 35 celery plants were inoculated from plantain containing the virus originally obtained from asters naturally infected with the disease, but only a single aster developed typical symptoms of yellows. Previously noninfective *T. montanus* recovered the virus from this diseased aster and transferred it to 1 of 4 healthy asters. Twelve asters and 27 celery plants were similarly inoculated from plantain containing the virus originally obtained from celery naturally infected with the disease, but only 1 celery plant developed yellows. The virus was not recovered from the experimentally infected celery plant by *T. montanus,* but was transferred to aster and celery by previously noninfective *C. divisa.*

TRANSMISSION OF YELLOWS BY THAMNOTETTIX GEMINATUS TO HEALTHY ASTERS AND CELERY

Fed on Naturally Infected Asters.—Although *Thamnotettix geminatus* was collected on asters under natural conditions, a high mortality of the adults occurred on small asters in the greenhouse when *T. geminatus* was transferred from large asters in the field. It was found that 6 lots

of 3 leafhoppers fed on 6 healthy asters died within a week, and all of the asters remained healthy as shown in table 6 (p. 356). In all probability the virus incubation period in the insects was not completed.

Bred on Naturally Infected Celery.—Thamnotettix geminatus collected on asters in the San Juan and Salinas valleys deposited eggs in potted celery plants naturally infected with yellows. The nymphs which hatched fed for a period of at least 2 weeks on the celery-yellows plants

TABLE 4

TRANSMISSION OF YELLOWS BY THAMNOTETTIX GEMINATUS TO SUCCESSIVE HEALTHY CELERY AND ASTERS AND RECOVERY OF VIRUS FROM EXPERIMENTALLY INFECTED PLANTS BY CICADULA DIVISA*

Number of *T. geminatus* transferred from infected celery	Successive celery and aster plants inoculated by *T. geminatus*						Virus recovered from experimentally infected plants and transferred by *C. divisa*	
	First set of celery	First set of asters	Second set of celery	Third set of celery	Fourth set of celery	Fifth set of celery	To aster	To celery
3	+	−	−	−	+	−	++	++
3	−	−	−	−	+	−	+	....
3	−	−	−	−	+	...	...	+
3	−	−	−	−	−	....	...	...
3	−	−	−	−	+	....	...	+
3	−	−	−	−	+	....	+	..
Total +	1+	0+	0+	0+	5+	0+	4+	4+
Total −	5−	6−	6−	6−	1−	2−	0−	0−

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted; ++ = virus recovered from 2 sets of experimentally infected celery.

and were then transferred in lots of 5 or 10 to 6 healthy celery plants. One of 6 celery plants developed symptoms of yellows. After the nymphs acquired the winged stage, 48 adults were transferred to 1 healthy celery plant, which also became diseased (table 6).

Bred on Asters and Celery Experimentally Infected by Cicadula Divisa.—Nymphs lived longer than adults on aster, and sometimes the nymphs acquired the winged stage on asters. Nymphs which hatched from eggs deposited in healthy celery were transferred to asters experimentally infected with yellows by *Cicadula divisa.* Nymphs and adults reared on diseased asters were transferred singly to 35 healthy asters with negative results. Likewise 2 lots of 5 adults and 2 lots of 20 adults failed to transmit yellows to 4 asters (table 6).

Eleven adults of *Thamnottetix geminatus* bred on celery experimentally infected with yellows by *Cicadula divisa* failed to transmit the virus to 11 healthy asters (table 6).

Adult *Thamnotettix geminatus,* collected on asters in the San Juan

and Salinas valleys, were fed for a period of 3 weeks on a celery plant experimentally infected with yellows by *Cicadula divisa*. Six lots of 3 leafhoppers each were transferred to successive healthy celery and aster plants until all of the insects were dead. The adults were fed on each celery plant for a period of 1 week and on each aster for 1 day. The results obtained are indicated in table 4.

Table 4 shows that from the first transfer (to 6 healthy celery plants) infection occurred in 1 plant which developed typical symptoms of yellows; in the second transfer (to asters) all of the plants remained healthy; in the third and fourth transfers (to celery) no infections occurred; and in the fifth transfer (to celery) 5 plants became diseased. In the fifth transfer 4 of the 5 infections occurred at the end of 8 weeks. The minimum virus incubation period in *Thamnotettix geminatus* is not known; in *Cicadula divisa* it was found to be 13 days.[8] The virus was recovered by previously noninfective *C. divisa* and transferred to healthy asters and celery from each celery infected by *T. geminatus*. The virus was also recovered by previously noninfective *T. geminatus* from 1 of the 6 celery plants infected with the yellows by this leafhopper.

Fed on Naturally Infected Celery and Celery Experimentally Infected by Cicadula Divisa and Thamnotettix Geminatus.—Tests were made on the transmission of yellows by lots of 1, 5, 10, 20, and 25 adults of *Thamnotettix geminatus* which were transferred in succession to one or more healthy celery plants. Some of the leafhoppers were collected on various food plants in the field and were fed for a period of 2 to 4 weeks on celery experimentally infected with yellows by *T. geminatus* or *Cicadula divisa*, or on celery naturally infected with the disease. *T. geminatus* which had been bred on celery experimentally or naturally infected with yellows were also used. The leafhoppers were transferred at the end of every 2 weeks to successive healthy celery plants until all of the insects were dead. Table 5 indicates the results obtained on the transmissions of celery yellows obtained with *T. geminatus* but does not show the number of negative tests. Table 5 also shows the recovery of the virus by *C. divisa* from some of the celery plants experimentally infected with yellows by *T. geminatus*, but all of the infected celery plants were not tested.

It is evident from table 5 that *Thamnotettix geminatus* transmitted yellows at irregular intervals, but infections occurred more often on the first celery plant. However, in one case where 15 leafhoppers were transferred to successive healthy celery plants at intervals of 2 weeks until

[8] Based on unpublished data.

TABLE 5

TRANSMISSION OF CELERY YELLOWS BY THAMNOTETTIX GEMINATUS TO SUCCESSIVE HEALTHY CELERY PLANTS AND RECOVERY OF VIRUS FROM EXPERIMENTALLY INFECTED CELERY BY CICADULA DIVISA*

Number of *T. geminatus* transferred from infected celery	Successive celery plants inoculated by *T. geminatus*								Virus recovered from experimentally infected celery and transferred by *C. divisa*	
	First set	Second set	Third set	Fourth set	Fifth set	Sixth set	Seventh set	Eighth set	To aster	To celery
1	+	....	...	...	...	....	....	.		−
1	+	....	..	..	.	....	....	..	.	−
1	+	....	....	....	...	...	....	...	..	−
1	+	−	−	....	...	.	....	...	.	−
1	−	+	−	...	...	.	....	....	.	. .
5	+	−	−	−	+	−	−	...	.	−
5	−	+	−	+	−	−	+	...	+‖	++§
5	+	−	−	−	.	....	....	....	+	+
5	−	+	+	−	....	....	....	....	+¶	−¶
5	+	−	−	..	...	....	....	....	...	+
5	+	−	−	....	....	....	....	....	.	+
5	+	−	−	....	....	....	....	..	.	−
5	−	+	−	....	....	....	....	....	+	+
5	+	−	....	....	....	....	....	....	+	+
5	+	−	....	..	...	....	....	....		+
5	+	−	....	....	....	....	....	....	+	+
5	−	+	...	....	....	....	....	...	+	+
5	+	−	.	...	....	....	..	...		−
5	+	...	...	...	....	....	..	..	.	−
10	−	−	−	−	+	−	−	....	+	....
10	+	+	−	−	−	−	−	....	++	+¶
10	+	−	−	−	−	−		....	+	+
10	−	+	−	−	−	−		...	.	+
10	+	+	−	−	...	....	...	..	.	−+
10	+	−	−	−	..	....	....	.		+
10	+	−	−	−	...	....	..	....		+
10	+	+	+	−	...	....	..	..	+++	+++
10	−	+	−	+	...	....	....	.	+¶	+
10	+	−	−	..	....	...	...		+	+
10	+	+	−	....	.	....	....	....	....	++
10	−	−	+	..	. .	...	....	....		+
10	+	−	−	..	..	..	..	..	....	+
10	−	+	..	..	...	...	..	. .		+
10	+	+	..	..	...	....	..	.	+¶	+
10	+	−	...	....	....	....	...	. .	+	.
10	+	+	....	..	..	....	.	.	+¶	+
10	+	....	....	....	. .	....	....	..	+	..
10	+	....	....	....	..	....	....	..	....	−
10	+	....	..	...	....	....	....	.	....	.
10	+	....	....	....	....	....	....	..	....	....
10	+	....	....	....	....	....	....	....	....	−
10	+	..	..	..	...	...	..	..	..	..
15	−	−	−	−	−	−	+	+	..	..
15	−	+	....	..	...	. .	...	....	+	+
20	+	−	−	−	....	....	....	....	+	+
20	+	−	−	..	. .	....	....	....	+	..
20	+	−	−	....	....	....	....	....	.	+
20	+	−	−	..	....	....	....	....	+	..
20	−	+	−	....	....	....	....	....	+	+
20	+	−	−	....	....	....	....	....	..	−
25	+	−	−	....	....	....	....	....	+	+
25	+	....	....	....	....	....	....	....	−	+
25	+	....	..	....	..	....	....	....	..	−
Total +	40+	15+	3+	2+	2+	0+	2+	1+	26+	34+
Total −	13−	25−	28−	13−	5−	7−	3−	0−	2−	15−

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted.
¶ Only one test made.
§ Only two tests made.

all of the insects were dead, infections were obtained with the seventh and eighth plants but not with the first 6 plants. This means that an infection was obtained at the end of 14 weeks.

One hundred and ten adults of *Thamnotettix geminatus* were transferred singly to 200 celery plants and only 5 plants, or 2.5 per cent, de-

TABLE 6

Summary of Results on Transmission of Yellows by Thamnotettix Geminatus to Healthy Asters and Celery

Source of virus	Asters inoculated	Asters infected	Asters healthy	Per cent infected
Fed on naturally infected asters	6	0	6	0.0
Bred on asters experimentally infected by *Cicadula divisa*	39	0	39	0.0
Bred on celery experimentally infected by *C. divisa*	11	0	11	0.0
Fed on celery experimentally infected by *C. divisa*	6	0	6	0.0
Total	62	0	62	
Percentage				*0.0*

Source of virus	Celery inoculated	Celery infected	Celery healthy	Per cent infected
Fed on naturally infected celery	7	2	5	28.6
Fed on celery experimentally infected by *C. divisa*	26	6	20	23.0
Fed on naturally infected celey and celery experimentally infected by *T. geminatus* and *C. divisa*	527	69	458	11.2
Total	560	77	483	
Percentage				*13.7*

veloped typical symptoms of yellows. Fifty lots of 5 insects each were transferred to 129 celery plants and 18 positive cases of yellows developed. In the next test 54 lots of 10 leafhoppers each were transferred to 151 celery plants, and yellows was transmitted to 31 plants. A small number of tests were made with larger numbers of leafhoppers as follows: 2 lots of 15 insects each transmitted yellows to 3 of 10 celery plants; 10 lots of 20 insects each to 9 of 32 celery plants; and 3 lots of 25 insects each to 3 of 5 celery plants. A total of 1,205 leafhoppers were tested by transfer to the first set of celery plants. Death of some of the insects occurred in the successive transfers. A total of 527 celery plants were inoculated by means of *T. geminatus* and 69 plants, or 11.2 per cent, developed symptoms of yellows (table 6). The transmission of celery yellows from all sources by *T. geminatus* averaged 13.7 per cent (table 6). The results on the transmission of yellows by *T. geminatus*, as summarized in table 6, show that a total of the 62 asters were inoculated but not a single case of aster yellows developed.

ADDITIONAL HOST PLANTS EXPERIMENTALLY INFECTED WITH YELLOWS BY THAMNOTETTIX GEMINATUS

Carrot Yellows.—Tests were made to determine whether *Thamnotettix geminatus* could recover and transmit the virus more readily from other host plants of yellows. The leafhoppers were commonly taken on carrots in the Salinas and Sacramento valleys. Nymphs and adults after feeding

TABLE 7

TRANSMISSION OF CARROT YELLOWS BY THAMNOTETTIX GEMINATUS AND RECOVERY OF VIRUS FROM INFECTED PLANTS BY CICADULA DIVISA

Variety	Plants inoculated	*T. geminatus* on each plant	Plants infected	Plants healthy	Incubation period in plant, days	Virus recovered and transferred from infected carrots by *C. divisa**	
						To aster	To celery
White varieties:							
Short white	1	5	1	0	33	—	—
	1	15	1	0	30	—	—
	1	20	1	0	36	—	—
	1	25	1	0	37	—	—
	4	1–25	0	4	....	....	....
White Belgian	1	25	1	0	43	—	—
	3	1–25	0	3	....	....	....
Orange varieties:							
Danvers Half Long	5	10–25	0	5	....	....	....
French Forcing	1	10	0	1	....	....	....
Long Orange	9	5–25	0	9	....	....	....
Oxheart or Guerande	7	5–20	0	7	....	....	....
Total	34	....	5	29	....	5—	5—
Average	....	....	....	....	35.8	....	....

* The minus sign (—) shows that no disease resulted.

on carrots experimentally infected with yellows by *Cicadula divisa* or on carrots naturally infected with the disease were transferred to healthy carrots. Table 7 indicates the results obtained.

Table 7 shows that 4 of 8 Short White carrots and 1 of 4 White Belgian carrots were experimentally infected with yellows by *Thamnotettix geminatus*. The leafhoppers failed to infect any of the 4 orange varieties of carrots. The incubation period of the disease in the plant varied from 33 to 43 days, with an average of 35.8 days. The virus was not recovered by *Cicadula divisa* from carrots infected with yellows by *T. geminatus*.

Thamnotettix geminatus failed to transmit yellows to healthy asters

and celery from 5 carrots of an orange variety naturally infected with the disease.

Hollow Crown Parsnip Yellows.—Twelve lots of 3 adult *Thamnotettix geminatus* each, after feeding on Hollow Crown parsnip (*Pastinaca sativa*) infected with yellows by *Cicadula divisa,* failed to transmit the virus to 12 healthy celery plants.

DISCUSSION

If aster and celery yellows are caused by two viruses, then *Cicadula divisa* and *Thamnotettix montanus* failed to separate them, and apparently only one virus is concerned. Host-range differences and overlapping of host ranges have been discussed in a previous paper by the author[15] and by Kunkel[9] and Smith.[17] Among the economic plants infected with California aster yellows by *C. divisa* and by *T. montanus* no host-range differences have been found.

Cicadula divisa transmitted the virus with greater efficiency than *Thamnotettix montanus* or *T. geminatus. C. divisa* transferred the virus from naturally infected asters to 48.3 per cent and *T. montanus* to 20 per cent of the healthy celery plants (table 1). In the recovery of the virus from experimentally infected celery in one experiment, *C. divisa* transferred the virus to 100 per cent of the healthy aster and celery plants while *T. montanus* failed to transmit the virus to healthy asters but transferred the virus to 44.4 per cent of the healthy celery plants (table 2).

SUMMARY

A summary of the results obtained on the transmission of yellows by *Thamnotettix montanus* and *T. geminatus* is given in tables 3 and 6.

It was demonstrated that *Thamnotettix montanus* is a vector of celery yellows under natural conditions.

The transmission of yellows by *Thamnotettix montanus* to asters averaged 2.9 per cent and to celery 26.1 per cent.

Thamnotettix montanus failed to transmit curly top to sugar beets.

The host plants experimentally infected by *Thamnotettix montanus* include, aster, celery, carrots, White London mustard, Prickly Winter spinach, Prizehead lettuce, and plantain or ribgrass (*Plantago major*). White London mustard is a new host plant of California aster yellows.

Thamnotettix geminatus failed to transmit yellows from naturally infected asters, and from asters and celery experimentally infected by *Cicadula divisa,* to healthy asters; but further investigation is being

made on this point. The transmission of yellows from all sources to celery by *T. geminatus* averaged 13.7 per cent.

Thamnotettix geminatus tested singly transmitted yellows to 2.4 per cent of the healthy celery plants.

The host plants experimentally infected with yellows by *Thamnotettix geminatus* were celery and Short White and White Belgian carrots.

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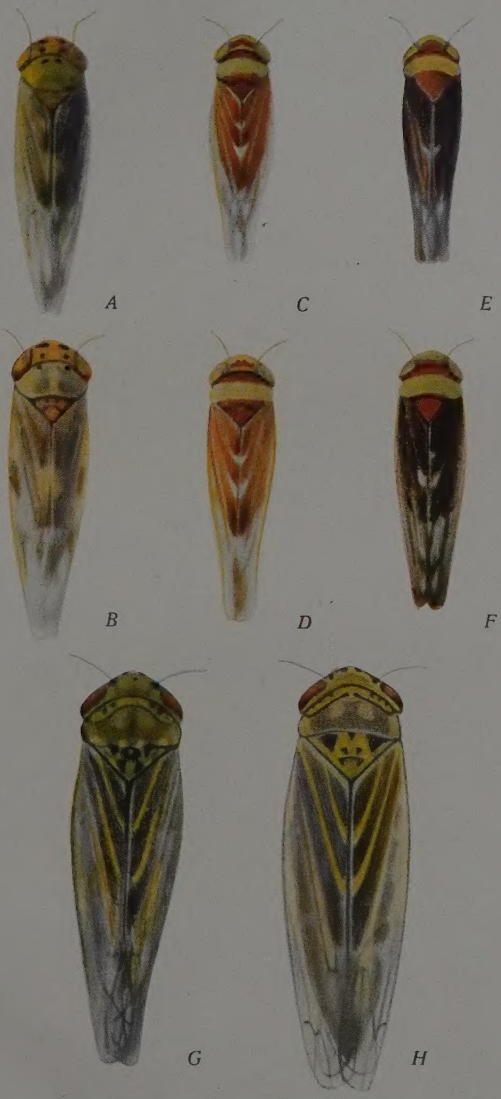

Plate 1.—*A*, *B*, *Cicadula divisa*; *C*, *D*, *Thamnotettix montanus*, adults of summer generation; *E*, *F*, *T. montanus*, adults of autumn generation; *G*, *H*, *T. geminatus*.